Roots as primary producers in below-ground ecosystems

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SUMMARY

1 Evidence from a variety of forest, shrub, and grassland ecosystems suggests that roots and mycorrhizas constitute 40–85% of total net primary production. The estimated fluxes represent a sizeable drain on the carbohydrate reserves of plants and comrpise a major route for the return of associated nutrients to the soil.

2 Very often these productivity estimates are rough approximations based on sequential biomass sampling, and fail to account for the simultaneous production and decomposition of roots during active periods of net biomass increase.

3 Inclusion of losses due to detritus production, exudation, and herbivory would improve these estimates.

INTRODUCTION

Primary production by vascular plants provides most of the organic materials fueling decomposition and other processes supporting soil organisms. Net primary production is the rate of storage of organic matter in plant tissues in excess of respiratory utilization during a given period (Odum 1971). Two general methods of determining annual net production exist. One, the gas-exchange approach, is based on measuring the rate of photosynthesis throughout the year and then subtracting concomitant respiration, and the other, the harvest approach, on measuring increases in biomass during a year. The latter method provides information of more direct interest to soil biologists, e.g. amounts of organic matter entering the soil and rates for decomposition and other processes. One variant of a commonly used expression summarizes the parameters used to calculate net primary production:

$$\text{net production} = \Delta B + L$$

where ΔB is the annual increment in biomass, L is the loss due to detritus production (e.g. leaves, branches, bark, inflorescences, seeds, and roots), exudation, volatilization, leaching and herbivory.

Accurate estimation of root parameters in the production equation has proven one of the most intractable tasks for soil biologists due to non-uniformities in the size and distribution of roots, the physical problems in separating roots from soil, and difficulties in collecting exudates and volatiles. As a consequence of these problems and the effort needed to measure root biomass, one approach for estimating net primary production has been to ignore below-ground parameters entirely or to estimate them indirectly. Newbold stated in 1967 that no accurate estimates of below-ground production in forests had been obtained and as recently as 1975 Whittaker & Marks, stated that 'the amounts of annual loss of root hairs and roots from plants in the field are almost unknown.' Leaf litterfall provided an obvious, easily measured process for the input of organic matter and associated nutrients to the soil and was believed to constitute the major route for the return of nutrients to the soil (Gray & Williams 1971; Heilman & Gessel 1963). If below-ground production was included it was estimated indirectly, based on the assumption that the ratio of production to mass must be similar for the root system and the shoot system (Andersson 1970; Kira & Ogawa 1968; Newbold 1967; Nihlgard 1972; Whittaker *et al.* 1979). The ratio of root production to mass was generally assumed to range from 20 to 100% of the above-ground ratio (Harris, Santantonio & McGinty 1980; Whittaker & Marks 1975). The use of indirect estimates has persisted. As recently as 1981, Pastor & Bockheim assumed the ratio of root production to mass to be equal to the ratio for above-ground biomass in the study of an aspen–mixed hardwood ecosystem.

This review examines the results of an alternative approach, the harvest method, for measuring root parameters and determining their significance in net primary production. Methods and assumptions in the measurements are examined; information available on production and loss parameters evaluated; and finally net primary production estimates for different forest and herbaceous ecosystems compared.

ESTIMATION OF PRIMARY PRODUCTION PARAMETERS

Biomass increment

Measurement of initial standing crops

The harvest approach for estimating root production employs measurements of changes in standing crops to determine the significance of root parameters in the net primary production equation. The first problem in this approach is devising a sampling scheme for measuring root biomass. Three basic factors have to be considered in sampling roots: (i) diameter of roots, (ii) spatial distribution, and (iii) temporal distribution. The roots of monocotyled~~e~~onous plants such as barley are small and fairly uniform, ranging in diameter from less than 0·1 to 0·7 mm (Russell 1977). After germination, the root system develops by repeated branching, producing seminal axes, nodal axes, first order laterals, and second order laterals. Ultimately, the root system occupies a soil volume determined in part by genetics, environmental factors, and plant density (Nye & Tinker 1977; Russell 1977). An acceptable sampling scheme must account for the variation in root density resulting from the interaction of these factors and temporal differences in the spread of roots through the soil. Distribution of the root system of the entire crop is of greater interest in ecosystems research than that of a single plant. Classification of roots by size is only of interest if the size classes reflect functional or spatial differences.

Classification or description of root system architecture is of more utility in forest ecosystem studies, due to the large size differences among different orders of tree roots and their associated functional differences. One commonly employed classification scheme for conifers divides roots functionally into those providing structural support for the tree, termed long lateral roots, and those active in the absorption of water and nutrients, termed short roots; the latter are often ectomycorrhizal (Fogel 1983). Lateral roots are generally subdivided into large and fine root categories on the basis of diameter; either 2 or 5 mm is often used as the upper diameter limit for fine roots. Complicating the functional classification of roots is the lack of short roots in the Cupressaceae, Taxodiaceae, and most angiosperms. Further complicating a functional classification is the inclusion of suberized, unsuberized, and endomycorrhizal roots in the fine root category for those species lacking short roots and inclusion of ectomycorrhizal and non-mycorrhizal roots in this category for species having short roots. From the standpoint of sampling, root systems can be considered to consist of two parts: (i) fine roots less than 2 mm in diameter, and (ii) structural roots, larger than 2 mm in diameter, which provide the framework supporting the fine roots.

Up to a dozen or more large lateral roots may arise irregularly from the stem base in conifers (Eis 1974; Fayle 1975), especially on steeply sloping ground, or approximately equidistantly around the stem (Deans & Ford 1983; Eis 1974; McMinn 1963). The horizontal spread of lateral roots varies with the size of crown, stocking density, and age of tree (McMinn 1963). Root density, diameter, and average depth of main lateral roots all decrease with distance from the stem (Hermann 1977; McMinn 1963). From 80 to 90% of structural root biomass is found within 1–1·2 m of the stem base in young red pine *Pinus resinosa* and sitka spruces *Picea sitchensis* (Deans 1981; Fayle 1975). Full occupation of the soil may take 10 years in Douglas fir *Pseudotsuga menziesii* (McMinn 1963) or up to 20 years in red pine (Fayle 1975). Most of the lateral roots are found in the upper 50 cm of soil with sinker roots reaching far greater depths (Fayle 1975; Deans & Ford 1983). The difficulty in severing large-diameter lateral roots precludes the use of coring techniques for biomass sampling. An additional problem results from the cross-sectional area of cores (generally less than 75 mm in diameter) being inadequate to sample roots present in low densities. As a consequence, biomass of large structural roots is best determined by excavation of whole trees or soil monoliths–laborious techniques very often resulting in only a small number of root systems being sampled. The data are often expressed as top to root ratios (Bray 1963) or as allometric equations relating root mass to stem diameter (Dice 1970; Ovington & Madgwick 1959).

Soil coring has been used extensively to measure fine root and mycorrhiza biomass since these roots are easily obtained by this method. Fine root density has been reported to be independent of stem proximity (Moir & Bachelard 1969), decreasing with distance from stem (Ford & Deans 1977; Roberts 1976), or reaching a maximum at 0·5–1·0 m from the stem (Persson 1980). Localized concentrations of roots may occur due to discrete patches of decaying organic matter or obstructions such as fragipans or cobbles (Fogel 1983). Most fine roots and mycorrhizas are found in the top 20 cm of the soil, depending on soil aeration and fertility (Fogel 1983). The discontinuous distribution of fine roots and mycorrhizas may require a large number of soil cores and/or batching of soil samples to reduce the variance in biomass to an acceptable level. Once cores have been collected, considerable time is spent separating roots from the soil by hand-sorting or by wet-sieving. The choice of separation technique affects the efficiency of recovery; wet-sieving yields estimates *c.* 30% larger than hand-sorting (Fogel 1983).

Available estimates suggest that tree root biomass comprises 15–25% of the total tree biomass, although individual estimates range from 9 to 44% (Fogel 1983). In grasslands and tundra, below-ground components of the plant may reach 75–98% of plant biomass (Dahlman 1968; Shaver & Billings 1975). Root biomass estimates for conifer stands less than 200 years old range from 3 to 85 Mg ha^{-1}; an estimated 209 Mg ha^{-1} has been reported for an old-growth Douglas fir stand (Fogel 1983). Root mass in stands of deciduous trees less than 200 years old ranges from 17 to 95 Mg ha^{-1} (Santantonio, Hermann & Overton 1977). Fine root estimates range from 1 to 12·6 Mg ha^{-1} with a mean of 5 (Fogel 1983). It is highly probable that mycorrhizas have not been included in the fine root estimates despite their importance in nutrient absorption (Fogel 1983).

Studies specifically mentioning ectomycorrhizas (total standing crop of active plus inactive mycorrhizas) indicate that they comprise up to 6% of the total tree biomass of Douglas fir (Fogel & Hunt 1983). Mycorrhiza standing crop estimates range from 1 to 25 Mg ha^{-1} (Fogel 1983), but the reports are difficult to compare due to differences in separation techniques, species, and whether total or active biomass is reported.

Root research in agro-ecosystems has focused on modelling nutrient absorption and competition among species. Root length rather than biomass has been the preferred parameter in many of these studies (Nye & Tinker 1977). Consequently very few standing crop estimates are available for comparison with forest ecosystems. Root biomass was estimated to be 16·2 Mg ha^{-1} in a native grassland studied by Dahlman (1968). Total dry weight averages 1·2 Mg ha^{-1} in a number of winter wheat cultivars, nearly equalling the shoot biomass of 1·25 Mg ha^{-1} (Gregory *et al.* 1978). Root biomass in soybean was considerably less than graminoid biomass; only reaching 0·6 Mg ha^{-1} 85 days after sowing (Sivakumer, Taylor & Shaw 1977).

Increment in standing crops

Annual biomass increment (ΔB) of large structural roots of trees has been estimated from changes in measured standing crops by the monolith method (Harris, Kinerson & Edwards 1977; Reichle *et al.* 1973), by large cores (Harris *et al.* 1977), or indirectly by increments in annual standing crops predicted by allometric equations relating root mass to stem diameters (Fogel & Hunt 1979; Kira & Ogawa 1968). An assumption in these approaches is that mass of large roots increases with time and that senescence and decomposition of large roots does not occur (Harris *et* *al.* 1977). A report by McMinn (1963) that the total length of structural roots increased with increased age in 10–55 year-old Douglas fir stands supports this assumption. Fayle (1975) on the other hand, observed that the terminal metre or more was dead in many of the main horizontal roots of 17 and 30 year-old red pines. Kolesnikov (1968) reports that large structural roots of apple begin to die when development of the tree begins to slow. Harris *et al.* (1977) commonly encountered dead roots >25 mm in diameter apparently associated with living trees. Several studies employing sequential harvesting have failed to detect any significant seasonal differences in the biomass of large conifer roots (Persson 1978; Santantonio *et al.* 1977). Monthly core data showed no consistent pattern of large root (>5 mm) production in a *Liriodendron* stand (Harris *et al.* 1977). When the root core data were grouped in quarterly periods, however, standing crop of *Liriodendron* roots increased sharply during spring and summer then declined during autumn. The difference between autumn and winter standing crops of roots >5 mm diameter was 800 kg ha^{-1} or 10·4% of the root standing crop. Production of roots >5 mm diameter in a Douglas fir stand, as estimated by difference in annual allometric estimates, was 2·1 Mg ha^{-1} or 4% of the root biomass (Fogel & Hunt 1983).

An alternative technique for estimating annual production in large roots involves measuring annual volume increment represented by growth rings—an extremely laborious process, but probably more acurate than estimates determined by difference in annual allometric estimates or in harvested standing crops (Fayle 1975; Deans 1981). Fayle (1975) found that current annual increment (CAI) of horizontal lateral roots in red pine reaches an initial plateau of over 0·6 dm^3 year^{-1} per tree around 15 years and that vertical root CAI levels off at 0·55 dm^3 year^{-1} around year 20. This volume increment represents an annual production of 1·4 Mg ha^{-1} or 4·8% of the root biomass if one assumes a specific gravity of 0·474 for wood and that stocking density is 2600 trees ha^{-1} (2 × 2 m spacing). Annual production of roots >5 mm in diameter, in a 16 year-old sitka spruce plantation (3800 trees ha^{-1}), was slightly more than double that of red pine at 3·2 Mg ha^{-1} (15·7% of root biomass) (Deans 1981). CAI of the red pine plantation was 0·54 kg per tree compared to 0·83 kg per tree in the sitka spruce plantation, despite the greater density of trees in the latter.

Production of fine roots and mycorrhizas of forest trees has been estimated primarily by summing significant increments in standing crops as estimated by soil coring. Production of conifer fine roots (Table 1) has been estimated to range from 3·5 to 11·0 Mg ha^{-1}. The few reports available for deciduous trees indicate a similar production of 5·4–9·0 Mg ha^{-1} (Table 1). These estimates are difficult to compare directly given the differences in stand ages, species composition, stocking density, and sampling methods. On a proportional basis, production of non-mycorrhizal fine roots ranges from 40 to 84% of root biomass.

Similar values have been reported in some herbaceous systems. Production in a native tall grass prairie (Table 1) was 5·1 Mg ha^{-1} compared to lower values of 0·6–4·3 Mg ha^{-1} in cultivated annuals. The difference between perennial and

TABLE 1. Annual production (Mg ha^{-1}) of fine roots in different ecosystems

Ecosystem	Age (years)	Production	Reference*
Coniferous forest			
Douglas fir	55	4·1–11·0	4
Loblolly pine	14	8·6	6
Red pine	53	4·1	7
Scots pine	5	3·5	8
Pacific silver fir	23	4·0	10
	180	6·5	10
Sitka spruce	16	5·3	3
Deciduous forest			
Yellow poplar	?	9·0	6
Oak–maple	80	5·4	7
Herbaceous			
Corn	<1	1·2–4·2	1
Soybean	<1	0·6	9
Tall grass prairie	?	5·1	2
Winter wheat	<1	1·1–1·2	5

* References: (1) Barber 1971; (2) Dahlman 1968; (3) Deans 1981; (4) Fogel & Hunt 1983; (5) Gregory *et al*. 1978; (6) Harris, Kinerson & Edwards 1977; (7) McClaugherty, Aber & Melillo 1982; (8) Persson 1978; (9) Sivakumar, Taylor & Shaw 1977; (10) Vogt *et al*. 1980.

annual herbaceous production might be due to lower plant densities in agroecosystems or perhaps greater utilization of soil volume by perennials in polycultures.

Production estimates for mycorrhizas are even more scarce than for other root classes. Annual biomass increment of live ectomycorrhizas in 23 and 180-year old stands of Pacific silver fir was 75 and 70% (1·5–1·9 Mg ha^{-1} of mycorrhiza biomass respectively (Vogt *et al.* 1980). Slightly lower proportions for live plus dead ectomycorrhizas of 61–68% (15·3–18·1 Mg ha^{-1}) were obtained in a 55 year-old Douglas fir stand (Fogel & Hunt 1983). Deans (1981) reported production of roots <5 mm diameter to be 5·3 Mg ha^{-1} or 108% of biomass. This estimate presumably includes a large proportion of mycorrhiza biomass since nearly all (99%) of the production was by roots 0–2 mm in diameter.

Biomass losses

Root losses

Several studies have failed to detect any significant decreases in the standing crops of large conifer and *Liriodendron* roots (Harris *et al.* 1977; Persson 1978; Santantonio *et al*. 1977), despite the reported presence of large dead roots in the *Liriodendron* stand, an apple orchard, and a red pine plantation (Fayle 1975; Harris *et al.* 1977; Kolesnikov 1968).

Large annual decreases or 'die-back' of the order of 30–90% occur in the

TABLE 2. Annual losses (% total wt) of fine root biomass in different forests

Ecosystem	Loss	Reference*
Deciduous forest		
European beech	80–92	4
Oak	52	5
Yellow poplar	42	2
Walnut	90	1
Coniferous forest		
Douglas fir	40–47	3,7
Scots pine	66	6

* References: (1) Bode 1959 in Hermann 1977; (2) Edwards & Harris 1977; (3) Fogel & Hunt 1983; (4) Gottsche 1972 in Hermann 1977; (5) Ovington, Heitkamp & Lawrence 1963; (6) Perrson 1978; (7) Santantonio 1979.

length, volume, or number of fine root tips for a number of quite different forest tree species, as has been known for some time (Fogel 1983). Graphs of 'white' root length versus time show decreases similar to those in forest trees for raspberry grown under irrigation (Atkinson 1973), apple trees (Head 1966), and pear trees (Head 1968). Annual biomass loss of fine roots, estimated by summing the significant decreases between peaks and troughs in monthly or seasonal standing crops, has revealed annual losses ranging from 40 to 92% in a number of forests (Table 2). In a Douglas fir ecosystem, combined annual fine root/mycorrhiza loss ranges from 14·6 to 18·8 Mg ha^{-1} (Fogel & Hunt 1983). These results indicate that fine roots and mycorrhizas are two to five times more important in returning organic matter to the soil than is leaf and branch litter (Fogel 1983; Edwards & Harris 1977).

Exudate losses

Root exudates include solubilized mucigel produced by the root cap, droplets secreted by root hairs, soluble materials from living cells, and sloughed fragments of cell walls. Carbohydrates, amino acids, organic acids, enzymes, auxins, vitamins, and other compounds (some of which stimulate or inhibit fungi, bacteria, and nematodes) have all been reported present in exudates (Russell 1977). Trees appear to exude more amino acids/amides than crop plants and comparable amounts of carbohydrates (Smith 1977). These compounds are important in the nutrition of rhizosphere organisms, but the amount of net primary production lost in exudates is difficult to estimate. The quantity of exudates is influenced by nitrogen levels, phosphorus supply, age of roots, rate of shoot extension, temperature, water stress, and the presence of micro-organisms (Russell 1977). Collection of exudates has been done in solution culture, with or without ballotini, under sterile conditions since microbes would metabolize compounds as they are released. An alternative approach in which the tops of plants are supplied with ^{14}C, and the proportion of labelled carbon collected in exudates measured, produces a minimum estimate since the amount depends on the balance between exudation and re-absorption of the label. Solution culture experiments with barley indicate that exudates may equal 7–10% of the shoot weight (Russell 1977). Under laboratory conditions, wheat plants supplied with ^{14}C for 21 days exuded 8·3% of the label in non-sterile soil compared to 6·2% in sterile soil (Russell 1977). The solution culture technique has been used under field conditions by Smith (1976) to collect exudates from unsuberized root tips of birch, beech, and maple. The roots were first severed and allowed to produce new tips. The tips were then inserted into tubes filled with sterile distilled water, and allowed to grow for 14 days. Only samples free of microbes were analysed for exudates. Exudates equalled 0·5–1·4% of the root weight. After adjusting for estimated number of root tips, length of growing season, and species composition of the stand under study, Smith calculated that annual production of exudates totalled 66·5 kg ha^{-1} in a northern hardwood forest. Exudates represented 43% of the new woody root tip mass in this study, or 1·1% of the live root biomass <3 mm diameter in a similar stand studied by McClaughtery, Aber & Melillo (1982). The results are interesting, but difficult to interpret since the technique employed permits collection only from axenic, unsuberized woody roots and does not include exudates from non-woody or mycorrhizal roots. In addition, exudates have only been collected late in the growing season and the growth of roots in a non-aerated solution is quite different from that in soil. The annual production of exudates by herbaceous species apparently has not been calculated on an ecosystem basis (Smith 1977).

Herbivory losses

Very few estimates exist for photosynthate losses below-ground to herbivory (Magnusson & Sohlenius 1980). Herbivory by nematodes and cicada in a mesic hardwood stand dominated by *Liriodendron* has been calculated by Ausmus *et al.* (1977). In this stand, 40% of the nematode population is composed of root-feeding species. Nematodes annually consume 8·5% of the living roots <5 mm in diam.: cicada larvae consume 1·4% of the fine root mass.

Phytophagous nematodes have also been studied in a 15–20 year-old Scots pine stand by Magnusson & Sohlenius (1980). In their study, root/fungal-feeding nematodes comprised 42% on average of the total number of nematodes and reached a maximum of 50–55%. Miscellaneous and bacteria-feeding nematodes dominated on a biomass basis, however. After assuming that half of the respiration of nematodes was by root/fungal-feeders and that half of the carbon utilized by this group was of fungal origin, consumption was estimated to be about 0·3% of the annual fine root production, an order of magnitude less than in the *Liriodendron* study. These losses are comparable to the 0.5–3.5% leaf weight losses to herbivory reported for deciduous forests (Bray & Dudkiewicz 1963; Reichle *et al.* 1973; Whittaker 1975).

NET PRIMARY PRODUCTION

Estimates from studies employing the harvest approach indicate that a large proportion of total net primary production (NPP) is channelled below-ground (Table 3). In forest ecosystems, below-ground production ranges from 40 to 73% of NPP. Below-ground processes account for 65–66% of NPP in shrub steppe communities and similar percentages of 50–85% have been reported for native grasslands.

The assumptions used in estimating the contribution of roots to net primary production should be examined to determine the reliability of the estimates and to identify possible areas for refinement. Estimating production by positive increments and loss by decreases in the standing crop of all roots irrespective of physiological status produces estimates generally regarded as conservative because steady-state conditions are assumed and mortality is not taken into account. This method of calculation assumes there is no acceptable method of distinguishing active (live) from inactive (dead) roots. In theory, production and loss estimates could be refined considerably by balancing changes in the standing crops of active and inactive roots (McClaugherty *et al*. 1982; Santantonio 1979). In practice, however, classification of the physiological status of roots has proved difficult. For instance, ectomycorrhizas pose a problem because of their small size (0·5–3·0 × 0·15–0·6 mm in diameter) and the possibility that the host tissue may continue to be physiologically active after the death of the fungal symbiont. Criteria for classifying active mycorrhizas are similar to those used for fine roots: turgidity, colour, integrity of root apex, association with mycelia, and the colour of sectioned host

TABLE 3. Contribution of roots (% total) to net primary production in different ecosystems

Ecosystem	Age (years)	Contribution	Reference*
Coniferous forest			
Douglas fir	55	73	3
Pacific silver fir	23	60	4
	180	71	4
Scots pine	14	60	1
Deciduous forest			
Yellow poplar	?	40	5
Shrub			
Atriplex steppe	?	65	2
Ceratoides steppe	?	66	2
Herbaceous			
Tall grass prairie	?	50	6
Short grass prairie	?	85	7

*References: (1) Ågren *et al*. 1980; (2) Caldwell & Camp 1974; (3) Fogel & Hunt 1983; (4) Grier *et al*. 1981; (5) Harris, Santantonio & McGinty 1980; (6) Kucera, Dahlman & Koelling 1967; (7) Sims & Singh 1971.

? = Not given or inappropriate.

tissues (Fogel 1983). Ectomycorrhizas from soil cores generally exhibit gradations in these characters, especially colour and turgidity, thus greatly increasing the possibility for errors in classification. Further errors may arise from incomplete recovery and improper handling, e.g. exposure to dry air (Lyford 1975). An alternative technique employing mitotic indexing of root meristems (Dunsworth & Kumi 1982) is unusable for field material due to the lack of intact root or mycorrhiza apices in many core samples.

Distinguishing active from inactive roots has also been a problem in herbaceous systems. Presence and absence of dividing cells in the root apex of grasses has been a criterion, but roots from soil cores often lack intact tips (Singh & Coleman 1973). Physiological status of some 'weeds' has been determined by measuring the electrical capacitance and resistance of roots, but this method is only suitable for roots of sufficient diameter to allow insertion of a probe (Singh & Coleman 1973). Vital stains such as congo red and tetrazolium have also been employed, but roots of various plant species react quite differently, apparently due to the age and physical properties of the roots as well as root cation exchange capacity (Böhm 1979). A modification of the vital staining technique involving the extraction of formazon (reduced tetrazolium) suffers the same problems as the tetrazolium vital staining technique (Sator & Bommer 1971; Singh & Coleman 1973). Carbon-14 labelling of roots under field conditions has also been tried (Sator & Bommer, 1971; Singh & Coleman 1973; Ueno, Yoshihara & Okada 1967). Singh and Coleman (1973) enclosed shoots of grasses in a plastic bag, exposed the tops to $^{14}CO_2$, extracted roots by coring, and then autoradiographed root segments for 4 weeks. Disadvantages of this approach include the time required to mount root segments and develop autoradiographs. The use of scintillation counting of pelleted root fragments reduces the time required to assay roots for activity but requires a highly significant correlation between disintegrations min^{-1} mg^{-1} dry weight of roots and percentage of active roots (Singh & Coleman 1973). Another carbon-14 technique provides an index of the productivity of root systems by measuring the reduction in the $^{14}C/^{12}C$ ratio for structural carbon of the roots following pulse labelling of the shoots with $^{14}CO_2$ (Caldwell & Camp 1974). The advantage of this approach is that the movement of labile carbon into and out of the roots does not affect the estimate. Under field conditions underestimation of production may result from a change in the proportion of living and dead roots between the initial and final root harvests. Underestimation may also occur if ^{14}C-compounds are translocated between harvests or by the release and subsequent reincorporation of ^{14}C into new structural material during the decomposition of labelled roots.

The tops of herbs and shrubs are fairly easily contained in plastic bags, but forests pose a more formidable problem. Herbs, shrubs, and tree branches in a forest stand could be isolated in bags and $^{14}CO_2$ injected into these bags. Many of the roots under a single tree would not be labelled, however, due to the intermingling of non-labelled roots from adjacent trees (McMinn 1963). An attractive solution would involve labelling roots directly in soil cores and then measuring vitality by scintillation counting after separation of roots from the cores.

Below-ground NPP estimates could be further refined by making adjustments for other loss parameters. Exudation is presently ignored due to the problems in its estimation, but the research by Smith (1977) indicates a possible underestimation of root production by 0·5–1·4%; experiments under laboratory conditions indicate the potential for much larger errors (Russell 1977). Volatilization is another possible source of underestimation, but is poorly understood and extremely difficult to estimate under field conditions. Herbivory estimates have little potential impact on NPP estimates since herbivory is accounted for in the root loss term as calculated by decrements in standing crops. Estimates of herbivory are important, however, in clarifying our knowledge of the structure and function of below-ground ecosystems.

CONCLUSIONS

Roots have been shown to play a major role in NPP in a number of different ecosystems. Root NPP ranges from 40 to 85% of total NPP with most of the available estimates falling in the range of 60–70%. The estimated fluxes represent a sizeable drain on carbohydrate reserves of plants for root production, and via senescence provide most of the organic material entering decomposition. The importance of roots in NPP has implications at several levels of ecological organization. If mechanisms controlling carbon cycling are to be understood, below-ground processes cannot be ignored. Similarly, below-ground processes may be crucial in nutrient cycling if the cycles are closely coupled to organic matter, i.e. nitrogen, phosphorus and potassium. Nutrient absorption models for either trees or annual crops are flawed if they are based solely on root production and fail to account for potentially large nutrient losses in root senescence and decomposition given the rapid turnover of fine roots and mycorrhizas. The magnitude of below-ground NPP has further implications beyond the ~~process and~~ ecosystem level. Many earlier regional and global carbon budgets (e.g. Reiners 1973; Rodin & Bazilevich 1967; Whittaker 1962; Whittaker & Likens 1973) are based on the questionable assumption that the ratio of root production to mass is 0·2–1·0 times that of shoot systems whereas the harvest approach suggests a more realistic factor would be 2·8 for *Liriodendron* (Harris *et al.* 1977) and 6·5–7·4 for Douglas fir (Fogel, pers. obs.).

The impact of the below-ground NPP research on our conception of ecosystem structure and function, while impressive, only represents a rough first approximation. Further refinement will depend on the development of techniques for measuring root vitality, exudation, and hyphal biomass of mycorrhizal fungi in the soil to supplement our understanding of production losses.

ACKNOWLEDGMENTS

Preparation of this paper was supported in part by National Science Foundation grant BSR 8215265.

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